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RIVER HYDROLOGY AND RIPARIAN WETLANDS: A PREDICTIVE MODEL FOR ECOLOGICAL ASSEMBLY

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Abstract. Riparian wetlands are under heavy pressure from hydrological changes produced by dam construction and water diversion projects. There has been ample documentation of the relationship between the extent of flooding and the composition of shoreline plant communities, yet we have few models that allow us to predict the impact of altered flooding regimes on riparian wetlands. In the humid temperate zone, river regulation commonly affects the distribution of two major vegetation types: wooded wetland and herbaceous wetland. The practice of reducing peak floods and augmenting minimum river flows is often followed by the succession of herbaceous to wooded wetland. We used logistic regression models to describe the distribution of wooded wetland as a function of all possible combinations of seven hydrological variables. The variables were chosen to reflect the depth, duration, and time of flooding and were calculated for four different time intervals (3, 7, 12, and 18 growing seasons). Our best model was a combination of two variables: the last day of the first flood and the time of the second flood. For three of the four time intervals, the vegetation type was correctly identified as herbaceous or wooded for >80% of the sample points. Our results suggest that models based on a few key environmental variables can be valuable tools in the conservation management of the vegetation of temperate and boreal zone wetlands.

Key words: boreal-zone wetlands; flood duration; herbaceous wetland; logistic regression; riparian wetlands; river regulation; temperate; time of flooding; vegetation type; wooded wetland.

INTRODUCTION

The structure and species composition of riparian vegetation constitute fundamental elements of the diversity of riparian ecosystems. The uniqueness of shoreline vegetation is especially evident in arid and semiarid regions where corridors of riparian forest rise above a landscape "barren of large woody plants" (Rood and Mahoney 1990). However, even in the forested watersheds of the humid temperate and boreal regions, riparian vegetation incorporates plant assemblages that differ markedly from the surrounding vegetation (Nilsson 1992, Malanson 1993). These assemblages are generally high in species numbers (Nilsson et al. 1988, Nilsson 1992) and encompass structurally distinguishable vegetation types, from trees through shrubs and herbaceous vegetation (Nilsson 1984, 1992).

This structural diversity and the importance of the herbaceous riverine marshes have been documented for the river shores of northern Sweden (Nilsson 1984, 1992) and Canada's eastern temperate zone (National Wetlands Working Group 1988), as well as the river deltas of Canada's boreal region (National Wetlands Working Group 1988). For example, the area of the Peace-Athabaska Delta is 3775 km^2 (National Wetlands Working Group 1988) of which 1200–1600 km^2 are herbaceous marsh or exposed mudflats (Townsend 1986). Although the value of herbaceous wetlands has often been measured in terms of animal habitat (Dirschl 1971, Townsend 1986, National Wetlands Working Group 1988), the flora merits attention for its high species numbers and rare plant component. Cases in point include the marshes along the Ottawa River, where 2–24 species have been recorded per 0.25 m^2 (Shipley et al. 1991) and the narrow herbaceous wetlands in the Tusket and Medway River systems, which support concentrations of Canada's threatened coastal plain flora (Keddy and Wisheu 1989, Wisheu et al. 1994)

The threat of river regulation to riparian vegetation has been well documented (Dirschl 1971, Johnson et al. 1976, Nilsson 1984, 1992, Bradley and Smith 1986, Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Johnson 1994). Dam construction and diversion projects have altered the hydrology of the majority of the watersheds of the Northern Hemisphere (Dynesius and Nilsson 1994). Fig. 1 indicates the thoroughness of our exploitation of Canadian Rivers alone. A major concern is the loss of wetlands and shoreline plant assemblages along these vast lengths of regulated shoreline (e.g., Johnson et al. 1976, Rood and Mahoney 1990, Stromberg and Patten 1990, Dynesius and Nilsson 1994). Indeed, much work has been done in modeling the dynamics of single dominant or threatened

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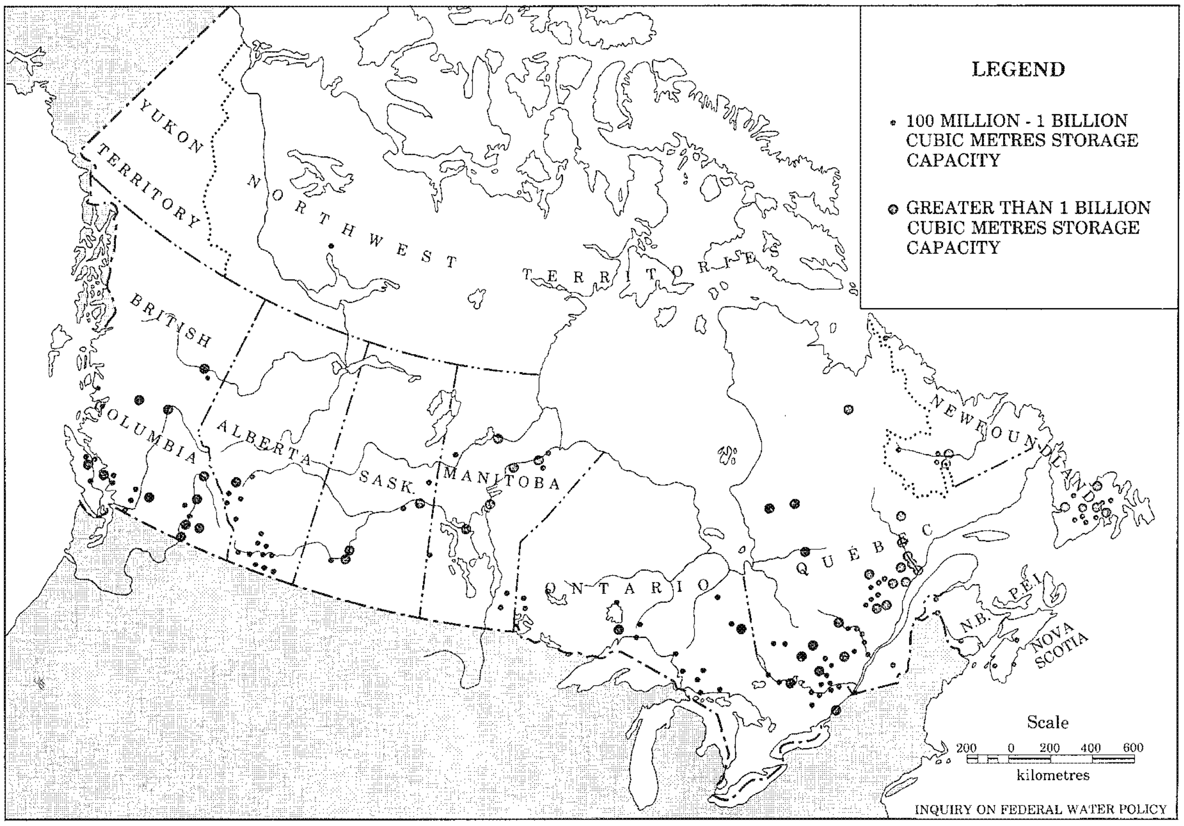

FIG. 1. An illustration of the scale of alteration of riparian hydrology in Canada. Circles indicate location of large dams. Large circles indicate a storage capacity $>10^9$ m^3; small circles indicate a storage capacity $>10^8$ m^3. (Source: Pearse et al. 1985. Reproduced with permission of the Minister of Supply and Services Canada, 1994.)

species, particularly in semiarid regions of western North America (Baker 1990, Rood and Mahoney 1990, Stromberg et al. 1993).

In the forested watersheds of more humid climates, however, river regulation poses the specific threat of changing the distribution of two major vegetation types—wooded and herbaceous wetland. Here, the alteration of hydrological regimes often results in a damping of seasonal fluctuation, with a reduced spring flood and augmentation of the low, late summer flows. These trends are evident in the water level records available from Environment Canada. The reduced water level fluctuations are often followed by the succession of herbaceous to wooded wetland (Keddy and Reznicek 1986). As early as 1945, Hall et al. (1945) described the disappearance of the emergent/wet meadow zone following water stabilization in the Tennessee Valley. A reduction in spring floods on the Peace–Athabaska Delta was followed by "unchecked succession" of herbaceous to wooded wetland (Dirschl 1971). Jaworski et al. (1979) described an extension of the wooded wetland into formerly herbaceous wetland along the shores of the Great Lakes during years of low water levels. A similar phenomenon has been associated with water diversions in Sweden (Grelsson and Nilsson 1980, Nilsson 1984). Conserving the diversity of the riparian wetlands of the boreal and humid temperate regions thus requires that we be able to predict which flood regimes will foster and which will prevent incursion by woody plants.

We need a simple model of the limits of wooded wetland, based on a small number of easily calculated variables that capture the impact of flooding. There is ample evidence that the time (Karr 1989, Johnson 1994) and duration (Yeager 1949, Hall and Smith 1955, Bedinger 1971) of flooding are important determinants of the limits of wooded wetland. These two factors have been identified as paramount in reviews of research on the flood tolerance of woody plants (Gill 1970, Teskey and Hinkley 1977). Water depth (Yeager 1949, Harris and Marshall 1963, Harms et al. 1980, Nilsson and Keddy 1988, Karr 1989) and frequency of flooding (Bedinger 1971, Nilsson and Keddy 1988) have also been identified as potential predictors. Several authors have designed measures of the duration of flooding from the data available for their study systems (Hall and Smith 1955, Bedinger 1971, Bell 1974, Nilsson and Keddy 1988, Auble et al. 1994, Johnson 1994). There has been less effort, however, to quantify the time of flooding and few comparisons of the predictive ability of the different hydrological variables one could imagine to be important; among the few reports are Nilsson and Keddy (1988)

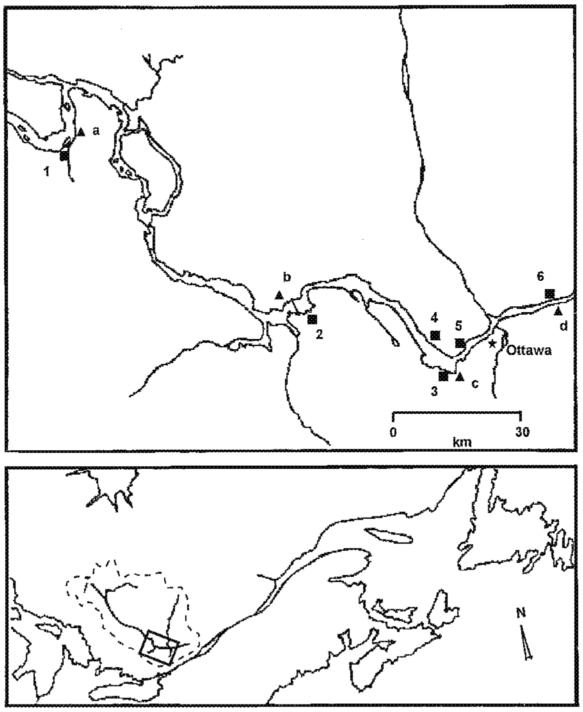

FIG. 2. Upper map. Squares, detail of Ottawa River study sites: 1, Westmeath Provincial Park; 2, Fitzroy Provincial Park; 3, Andrew Hayden Park; 4, Breckenridge Marsh; 5, Lucerne Boulevard; and 6, Masson. Triangles, location of water gauges: a, Town of Westmeath; b, Chat Falls Dam; c, Brittania Bay; and d, Cumberland. Adapted from Day et al. (1988). Lower map. Eastern Canada showing the Ottawa River drainage basin with rectangular inset of study region.

and Johnson (1994). We have therefore selected a set of hydrological variables, including several measures of the time of flooding. Our goals were (1) to identify the best predictors of the lower limit of wooded wetland, (2) to identify the range of these predictors in which there is a low probability of dominance by woody plants, and (3) to identify the period of time over which these variables would be effective.

METHODS

Study sites

The Ottawa River (mean annual discharge >1000 m^3/s) is typical of large rivers in the eastern temperate region in the extent of regulation and the occurrence of herbaceous wetlands; some shoreline marshes are as wide as 200 m. The first dam projects, in the early 1900s, were primarily flood control measures (Legget 1975). Subsequent hydroelectric projects have reduced the natural fluctuation in water levels by as much as half (Legget 1975), while leaving the general pattern of spring flood and lower late summer flows intact.

We examined a 200-km portion of the Ottawa River between Westmeath, Ontario (45°46′ N, 76°55′ W) and Cumberland, Ontario (45°31′ N, 75°25′ W), locating wetlands that were near water gauges (Fig. 2). Six such sites were found, four of which (Fitzroy Provincial Park, Westmeath Provincial Park, Andrew Hayden Park, and Masson) were judged to be sufficiently close (1–5 km) to gauging stations for direct use of gauge records.

A fifth site (Breckenridge Marsh) was 15 km from the nearest gauge. A small set of rapids separated a sixth site (Lucerne Boulevard) from a gauging station, although the actual distance was <2 km. Calibration curves (r^2 = 0.98 and r^2 = 0.96, N = 10) indicated that there were only small differences between fluctuations in water levels measured on regular visits to these sites and fluctuations recorded nearby at the Brittania gauge; thus, the gauge records were adjusted accordingly.

Records of the daily mean water level for the period from 1974 to 1992 were obtained from the Water Survey Division of Environment Canada and from Ontario Hydro. There were missing data, amounting to <2%, from two gauges. These values were inferred from calibration curves (r^2 = 0.99 and r^2 = 0.96, N = 222) based on records from gauges located upstream.

We were aware of the importance of disturbance on the distribution of shoreline vegetation and included subjective classifications of the slope as gentle or steep, and of the degree of exposure to wave and channel action as protected, moderate, or strong.

Dependent variable

The dependent variable was simply the presence or absence of woody cover, as determined by locating the boundary between wooded and herbaceous wetland. This boundary was defined as the base of the woody plants at the lowest limit of continuous cover by woody species. We sought to minimize the confounding role of disturbance by restricting the study to portions of shorelines where there was 100% cover by vegetation and where there were no signs of erosion near the boundary between the wooded and herbaceous wetland.

Data were collected during the growing season of 1993. At each site, we located up to 21 random points (5–7 points/80 m) along the shoreline. The sample size was smaller at some sites due to the size of the wetland or to local disturbance, such as footpaths.

At each point, the lower limit of continuous cover by wooded wetland was identified, the species noted, and the elevation of the point measured with respect to the water level. Water level readings for the time of sampling (within the hour) were either provided or calculated for the gauges described in *Methods: study sites*. At one site, it was necessary to refer to a daily mean. Monitoring of the stage at this site indicated that there was little fluctuation throughout the day of sampling.

These measurements of the elevation of the boundary were used to generate new pairs of elevation measurements with known vegetation type. The first datum would be a point in the wooded wetland (original el-

TABLE 1. Hydrological variables with abbreviations.

Abbreviation	Variable
gs	fraction of the growing season during which flooding occurred
ld	last day of the first flood
lsec	length of the second flood
md	mean depth of flooding
nf	number of floods per growing season
dbf	number of days of drawdown preceding midseason floods
tsec	time (first day) of the second flood

evation plus 5 cm), the second, a point in the herbaceous wetland (original point minus 5 cm). The independent variables were therefore descriptors of flooding at each of these new points. The horizontal distance associated with an elevation change of 5 cm varied from <1 m to >10 m.

Independent variables (hydrological)

A set of seven hydrological variables (Table 1) were calculated for each of the data points. The variables were selected to reflect the depth, duration, time, and frequency of flooding. The fraction of the growing season flooded was an obvious choice, given its straightforward calculation and prominence in the literature (Hall and Smith 1955, Bell 1974, Malecki et al. 1983, Nilsson and Keddy 1988). The only potential for ambiguity lies in the arbitrary definition of the growing season (Hall and Smith 1955, Malecki et al. 1983, Nilsson and Keddy 1988). We addressed this by using the 5.5°C rule (Grandtner 1966), an accepted practice for forests of Quebec and Ontario (Ontario Ministry of Natural Resources and Environment Canada 1984, Le Groupe Dryade 1985). The mean depth of flooding (Yeager 1949, Harms et al. 1980) and the number of floods per season (Phipps 1979, Nilsson and Keddy 1988) were selected as the most straightforward measures of the depth and frequency of flooding. Finally, we wanted to test for the impact of the time of flooding and of a possible second and/or midseason flood, so we included the end of the first flood, the beginning and length of the second flood, and the duration of the drawdown preceding any midseason flood. Midseason was defined as between day 90 and day 120 of the growing season. An eighth variable, the beginning of the first flood (Nilsson and Keddy 1988), was omitted as there was little variation in its value; points were generally flooded on the first day of the growing season. Calculations were based on daily averages of water levels. Drawdowns of only one day were thus considered questionable events and were ignored in assessing the duration of flooding.

The values for the variables were averaged over four intervals—the 3, 7, 12, and 18 growing seasons previous to the collection of data. The shortest interval is the time between onset of high water levels and dieback of woody plants, as described by Jaworski et al. (1979). The longest interval is the period identified as the requirement for succession of herbaceous wetland to wooded wetland in the Great Lakes system (Painter and Keddy 1992) and close to the 17-yr interval for succession from sedge meadow to low shrub in the Peace-Athabasca Delta (Peace-Athabasca Delta Project Group 1973).

According to conventional interpretation of the 5.5°C rule, the start of the growing season occurs when the mean daily temperature exceeds 5.5°C for five of seven days, and ends when the mean daily temperature fails to exceed 5.5°C for five of seven days. A climatic map of Canada (Canada Centre for Mapping 1990) indicated that all but the Westmeath site were in the same zone. Records from the Ottawa International Airport (45°19′ N, 75°40′ W) were used to calculate the growing season for these five sites. The beginnings and endings of the growing season were averaged over the 18-yr interval. Records from the Petawawa weather station (45°57′ N, 76°14′ W) were used to determine the growing season at Westmeath. Data were averaged over only 16 yr due to gaps in the records. We used the mean rather than the yearly parameters of the growing season for the generality it offered in the interpretation and application of results.

Independent variables (site variables)

Although site selection was designed to minimize the effect of disturbance, we decided to test for effects of exposure to waves or destructive floods by calculating three additional variables for each of the study sites: (1) effective fetch, (2) effective fetch multiplied by average wind speeds and frequencies, and (3) peak flow. A fourth variable, soil drainage, was included in the analysis as we were concerned about differences in the impact of duration of flooding depending on substrate. These variables were not significant in any of our regression models and will not be discussed further.

Analysis

Analyses were conducted separately for each of the four time intervals: 3 growing seasons (1990 through 1992), 7 growing seasons (1986 through 1992), 12 growing seasons (1981 through 1992), and 18 growing seasons (1975 through 1992). The analysis consisted of four steps:

1) Pearson product-moment correlations for pairs of flood variables were obtained using Sigmastat for DOS (Jandel Scientific 1992).

2) Logistic regressions (logit function) performed by SAS (SAS Institute 1987) were used to model (1) each hydrological variable in combination with the four site variables (fetch, fetch adjusted for wind speed and frequency, peak flow, and soil drainage) and (2) all possible combinations of hydrological variables. The

TABLE 2. Correlation of variables. Matrix of Pearson product-moment correlation coefficients for hydrological variables.

Variable	gs	ld	lsec	md	nf	tbf	tsec
gs	1.00						
ld	0.83 ***	1.00					
lsec	−0.35 ***	−0.52 ***	1.00				
md	0.13 (0.053)	0.30 ***	−0.060 (0.38)	1.00			
nf	0.64 ***	0.52 ***	−0.33 ***	0.019 (0.78)	1.00		
tbf	−0.60 ***	−0.67 ***	0.34 ***	−0.21 **	−0.57 ***	1.00	
tsec	0.62 ***	0.73 ***	−0.54 ***	0.075 (0.27)	0.22 ***	−0.48 ***	1.00

Note: Probability values are in parentheses, unless **, $P < 0.01$, or ***, $P < 0.001$; $N = 222$. Abbreviations as in Table 1.

presence or absence of woody cover was the dependent variable.

Four criteria were selected for evaluating the models. First, models were compared by examining the amount of deviation remaining. The best model had to have one of the lowest Akaike Information Criteria (AIC), a statistic that is analogous to the residual sums of squares of linear regression models (Hosmer and Lemeshow 1989). Second, we compared the accuracy of models, defining accuracy as the percentage of the original data correctly identified by the model as having woody or herbaceous cover. Third, we favored models that were consistently among the better models over the four time intervals. Finally, we chose the simplest model in cases where there were only small differences in the measures of the first three criteria.

The best model was used to plot the probability of occurrence of woody cover at various combinations of the component variables, to form a set of testable predictions.

3) After selection of the best models, dummy variables (Kleinbaum et al. 1988) were introduced to test for site differences for the time intervals where prediction was accurate. In addition, a separate series of logistic regressions, with hydrological variables only, were carried out for each site for the time interval with the best results. The number of variables in the site-specific models was limited to one or two, as site data represented small subsets ($N = 32$–42) of the combined data ($N = 222$). Results were compared for consistency between sites and with the best model from the combined data.

4) Finally, the diagnostic procedures available in SAS were used to identify (1) data that were not well explained by the model (Pearson residual), (2) data that had the greatest impact on the disagreement between the model and original data (DIFCHISQ), (3) data that had the greatest effect on the parameter coefficients (DFBETAs), and (4) data that had the largest effect on the maximum likelihood estimates (C and CBAR). A large portion of such data from one site would signal a problem with grouping points from different sites.

RESULTS

We found nine woody species at the boundary between wooded and herbaceous wetland: *Acer saccharinum* L., *Myrica gale* L., *Salix discolor* Muhl., *Salix nigra* Marsh, *Fraxinus pennsylvanica* Marsh, *Cornus stolonifera* Michx., *Cephalanthus occidentalis* L., *Alnus rugosa* (DuRoi) Spreng., and *Spirea alba* DuRoi. *Acer, Myrica,* and *Salix* were by far the most common genera. *Alnus rugosa* and *Spirea alba* were seen only rarely.

The only steep slopes encountered were portions of the shoreline at Fitzroy Provincial Park. This site included the most exposed shores, and portions of shoreline had to be excluded due to disturbance or removal of vegetative cover by wave action and human activity. The greatest range in exposure, from protected to exposed, was at Masson and Lucerne Boulevard.

Significant correlations

The average values for variables were calculated for growing seasons of 194 d (April 16 to October 26) for five of the sites and 184 d (April 19 to October 19) for Westmeath Provincial Park. As there were few midseason floods, our measure of the dry period before the midseason flood (dbf) was 0 for most of the points when averaged over intervals of only three or seven growing seasons.

The hydrological variables were strongly correlated (Table 2), with similar patterns over the four intervals. The highest correlation, $r = 0.83$ ($P < 0.001$), occurred for the relationship between the last day of the first

TABLE 3. The first three columns present the best one-, two- and three-variable models for each of the four time intervals. The last column includes the results for fraction of the growing season flooded (gs) and time of the second flood (tsec), for the intervals where it was the second-best two-variable model. Abbreviations for other variables are in Table 1.

	Number of variables in model			
Time interval	1	2	3	2
18-yr interval				
Variables included	nf	ld,tsec	ld,gs,tsec	gs,tsec
AIC score	279	214	212	258
Accuracy (%)	69.4	81.1	81.1	73.0
12-yr interval				
Variables included	nf	ld,tsec	ld,tsec,lsec	gs,tsec
AIC score	287	156	157	219
Accuracy (%)	64.4	86.0	86.5	77.0
7-yr interval				
Variables included	tsec	ld,tsec	ld,tsec,lsec	gs,tsec
AIC score	287	172	164	222
Accuracy (%)	61.3	81.1	83.3	75.7
3-yr interval				
Variables included	tsec	gs,tsec	ld,gs,tsec	
AIC score	279	276	267	
Accuracy (%)	66.2	56.8	67.6	

flood (ld) and the fraction of the growing season flooded (gs). The nonsignificant correlations generally involved the mean depth of flooding (md).

Best model

The best model combined two hydrological variables, the last day of the first flood (ld) and the time of the second flood (tsec). Its AIC score was the lowest or close to the lowest among the models and it was consistently accurate (>80%) over all but the 3-yr interval (Table 3, column 2). The probability of occurrence (p) of wooded wetland was calculated for different values of ld and tsec (Fig. 3) using the regression equations from the model for the 12-yr interval [$\ln(p/(1-p)) = -0.23(\text{ld}) + 0.16(\text{tsec}) - 1.42$]. A probability of ≥0.70 was considered high while a probability of ≤0.30 was considered low. Using these criteria, all but 18 of the 222 points were correctly classified, or were in the intermediate range of probability (36 points). Of these, the 8 points that were erroneously described as wooded wetland were from Masson and four of the points that were incorrectly designated as herbaceous wetland were from Lucerne Boulevard. As mentioned, both these sites included the extremes of protected and exposed shoreline in our sample.

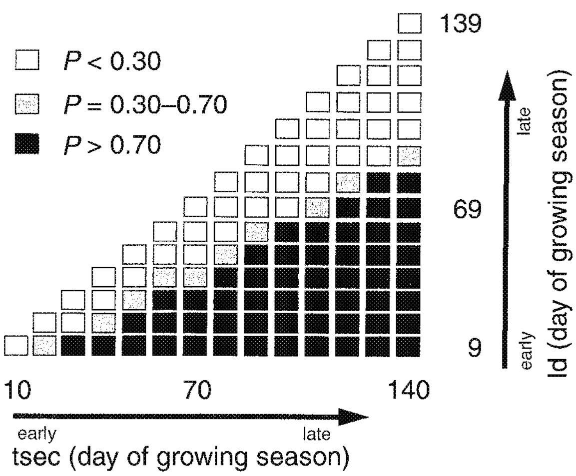

FIG. 3. The probability of occurrence of woody cover as predicted by the day of the growing season on which the first flood ends and the day on which the second flood begins. Parameters are taken from the 12-yr interval. Abbreviations: tsec, time of the second flood; ld, last day of the first flood.

The second best model, also composed of two variables, combined the fraction of the growing season flooded (gs) and time of the second flood (tsec). It was the best model for the 3-yr interval and always among the best for the other intervals. Its AICs and accuracy are included in the last column of Table 3 to allow comparisons with the model composed of ld and tsec, as well as with the best three-variable model.

Two other trends emerged from the analysis. First, the better models were all combinations of two variables. No single hydrological variable yielded a model with an accuracy >70% or an AIC <250 (Table 3, column 1). Further, models based on three or more hydrological variables had AIC scores that were only slightly lower than the value for the best two-variable model and were only one or two percentage points more accurate, with the exception of the 3-yr interval (Table 3, column 3).

Second, no model based on the 3-yr interval performed well. The accuracy never surpassed 70% and the AIC scores were all >250. Best results were obtained using the 12-yr interval, though they did not differ greatly from the 7- and 18-yr intervals.

Site differences

Three intervals (7, 12, and 18 yr) led to accurate models and were thus chosen for further analysis; dummy variables were used for sites in a series of logistic regressions. The number of site differences for the best model (ld, tsec) increased with the length of the interval considered. One site, Lucerne Boulevard ($\chi^2 = 3.88$, $P = 0.049$), was slightly aberrant for the 7-yr interval. For the 12-yr interval, two sites were significantly different: Lucerne Boulevard ($\chi^2 = 6.21$, $P = 0.013$) and Fitzroy Provincial Park ($\chi^2 = 6.72$, $P = 0.0095$). There were four site differences for the 18-yr interval; Lucerne Boulevard had the highest chi-square value ($\chi^2 = 14.18$, $P < 0.0001$). The chi-square values for tsec ranged from 43.97 to 49.81 ($P < 0.0001$) and for ld, from 39.44 to 46.76 ($P < 0.0001$).

In combinations of gs and tsec, only Fitzroy Provincial Park was significantly different for the 7-yr interval ($\chi^2 = 24.08$, $P < 0.0001$) and the 12-yr interval ($\chi^2 = 29.76$, $P < 0.0001$). Both Fitzroy Provincial Park ($\chi^2 = 30.08$, $P < 0.0001$) and Lucerne Boulevard ($\chi^2 = 5.98$, $P = 0.014$) were significant site variables for the 18-yr interval.

Logistic regressions were performed by site, using data from the 12-yr interval. The time of the second flood was the best single variable for four of the sites. Two-variable models always had greater accuracy and lower AIC scores, and the best model at every site included the time of the second flood (tsec). The last day of the first flood (ld) and the fraction of the growing season flooded (gs) were the second components of the best models for three and two sites, respectively. The mean depth of flooding (md) was the second component at one site.

Diagnostics

The points identified by the SAS diagnostics (Pearson residual, DIFCHISQ, DFBetas, C, and CBAR) did not indicate that any single site was problematic. A set of 10 data points were identified as extreme values by one or more of the diagnostic tests. These points came from three sites: Fitzroy Provincial Park, Masson, and Lucerne Boulevard, and represented <5% of the total data.

Discussion

General trends

One model emerged as best: the combination of the last day of the first flood (ld) and the time of the second flood (tsec). Here we have a simple, testable model that could provide a tool for maintaining wetland area and diversity.

The parameters from the logistic equation [$\ln(p/(1 - p)) = -0.23(\text{ld}) + 0.16(\text{tsec}) - 1.42$] indicate the direction of the effect of each of the two variables. The negative coefficient for ld indicates that the longer the first flood, the lower the probability of occurrence of woody cover. Conversely, the later the beginning of the second flood, the greater the probability of woody cover. Although both variables are continuous, we have arbitrarily chosen threshold probabilities of 0.7 and 0.3 to predict when wooded wetland would be present or absent. The ranges of ld and tsec that coincide with these high and low probabilities are depicted in Fig. 3. Based on these criteria, we do not expect woody cover if the first flood lasts >80 d. If the first flood were shorter, then woody cover may or may not occur, depending on the time of the second flood. The probability of occurrence increases with shorter first floods and later second floods.

Time of the second flood

The time of the second flood is a prominent variable in the most accurate of the multivariate models and is one of the best single predictors. It is not surprising that the time of flooding is significant, as it is a standard entry in lists of factors affecting the survival of woody plants (Gill 1970, Teskey and Hinckley 1977). However, flood events are commonly separated on a coarse time scale; that is, they are classified as occurring either during the growing season or during the dormant season (Hall and Smith 1955, Gill 1970, Teskey and Hinckley 1977, Karr 1989). The impact of the second flood within the growing season is striking, in part because it has received so little attention. The mechanism behind the role of later floods is not clear. However, studies on seedlings of floodplain tree species have revealed some pertinent trends. Streng et al. (1989) found that species with light seeds generally emerge early in the season, and the earlier the time of emergence, the higher the probability of survival. The higher survival rates were attributed to canopy conditions and better light availability; hence, greater opportunity for photosynthesis. Higher rates of photosynthesis lead to larger plants, thereby improving the probability of surviving adverse conditions.

A similar line of reasoning offers an explanation for the effect of the second flood at our sites. It is generally accepted that flooding during the growing season adversely affects the growth of most tree species (Kozlowski 1984). If a second flood occurs early in the growing season there is little time for the plants to recover, less if the first flood has lasted long. In fact, if the second flood begins shortly after the end of the first flood, it represents simply an extension of adverse conditions. If the combined flood period is long enough, it may surpass the tolerance of seedlings, or even mature trees. If, on the other hand, the first flood ends early and the second begins late in the season, then there is a period of favorable conditions. The longer the interval, the greater the chance that the plant will have recovered sufficiently to survive a second adverse period. Thus, the greater the period between the end of the first flood and the onset of the second

TABLE 4. Mean annual discharge, management, and time and approximate magnitude of second flood for eight Ontario rivers, based on 1990 hydrological records (Environment Canada). The magnitude of the second flood is based on discharge; where only water levels were provided the magnitude was not estimated.

River	Discharge (m^3/s)	Management	Time and approximate magnitude of second flood
Holland	1.7	regulated	late May
Bighead	5.1	regulated	late June, early July, six-sevenths of first peak
Mississippi	30.7	regulated	continual decrease in discharge over the growing season
Pic	39.1	natural	late June, one-third of first peak
Magnetawan	50.4	regulated	late May
English	58.1	natural	continual decrease in discharge over the growing season
St. Clair	175.94	regulated	no fluctuation in discharge
North	···	···	small second peak in late June, early July

flood, the higher the probability of occurrence of wooded wetland.

Effect of first flood

The end of the first flood is strongly correlated with the fraction of the growing season flooded and is therefore consistent with the importance assigned to duration of flooding in the literature (e.g., Yeager 1949, Hall and Smith 1955, Bell 1974). In fact, replacing the last day of the first flood with the fraction of the growing season still yields a reasonably accurate model.

The critical period of 80 d of flooding represents 41–43% of the average growing season. This range is consistent with the results of Hall and Smith (1955), who found that floods surpassing 40–45% of the growing season (April 1 to October 1) prevented healthy growth of the most tolerant species in their study (*Planera aquatica*, *Salix nigra*, and *Quercus lyrata*). Their study site in Tennessee did not include the remarkably flood tolerant *Taxodium distichum*. Bedinger (1971) also mentions a maximum of 40% in his study of the White River flood plain in Arkansas. However, comparisons with our results are difficult, as he used the year and not a defined growing season as his study period.

Despite the agreement of our results with studies of the flood limits for mature trees, the range that we have identified is more likely a threshold for seedling establishment, as we rarely saw unhealthy adult trees. Our interpretation is supported by Gill (1970), who suggests that flooding that lasts longer than 40% of the growing season prevents colonization by woody plants. While 36–38% of the growing season is a reasonable range to suggest for the flood tolerance of woody plants in our region, our field observations indicate that we have modeled the barrier to establishment of seedlings rather than the survival of adult trees.

The high correlation between ld and gs points not only to the importance of flood duration, but it indicates that the first flood accounts for most of the flooding that occurs during the growing season on the Ottawa River. The pre-regulation cycle of spring floods followed by lower summer levels is intact, though dampened. This cycle may be essential to the regeneration of many of the woody species of riparian zones, hence to the maintenance of the wooded wetland. We have described the problem of conversion of herbaceous to wooded wetland. However, flood regimes can be altered in a manner that threatens populations of woody species. For example, the seeds of both *Acer saccharinum* and *Salix nigra* are released in spring and lose viability quickly under dry conditions (Fowells 1965). The moist substrate that is exposed as spring floods recede is a requirement for germination. River regulation can eliminate the conditions necessary for regeneration and thus threaten the persistence of dominant species or entire vegetation types in our landscape. Cases in point include the reduction in habitat area for pioneer species in the Missouri River system (Johnson et al. 1976) and the decline in populations of *Populus* species along rivers in western North America following dam construction (Rood and Mahoney 1990). Our model is based on the assumptions that the conditions required for the regeneration of woody plants are present and that it is the herbaceous wetland that is threatened.

Implications for conservation management

Our findings have at least four implications for conservation management. First, we have identified three key predictors, ld, gs, and tsec that can be used in two combinations (ld and tsec or gs and tsec) to predict the occurrence of wooded wetland. We have also identified the ranges of these predictors where wooded wetland is likely to be present (Fig. 3), as well as an appropriate time frame for calculations. Our model has not yet been tested on other rivers and the results should be treated with caution.

Second, we have demonstrated the importance of the time of the second flood. This was consistently identified as a key predictor, yet has received little attention in the modeling of riparian vegetation to this point. A cursory examination of the 1990 hydrological records for eight Ontario Rivers, chosen randomly, reveals that a second flood is a common event on our rivers (Table 4). Further, these floods are unlikely to attain the magnitude of the first flood, which is usually associated with snow melt. They therefore offer the advantage of being biologically meaningful and potentially more manageable flood events.

Third, the accuracy of the two-variable model suggests that a small number of predictors can provide guidelines for conservation management of major vegetation types. Moreover, we were able to formulate quantitative guidelines with definable margins of error (Fig. 3) by using regression equations to assign probabilities for different management scenarios.

A fourth outcome of our study is the emergence of a potential, quantitative criterion for application of the model, the strong correlation between ld and gs. We may find that our model is more accurate, or only accurate, where the first flood represents a large percentage of the total flooding. We believe that most rivers in the eastern temperate and boreal regions would meet this criterion, due to the major role of snow melt. However, it might point to problematic applications. Quantitative criteria are seldom identified in riparian models; work is often based on one site (Franz and Bazzaz 1977, Phipps 1979, Poiana and Johnson 1993, Ellison and Bedford 1995) or one river system (Auble et al. 1994, Johnson 1994) with the assumption that the results may be applied to qualitatively similar sites. We believe that it would be worthwhile to consider that there may be a small number of categories of rivers (two to four), identifiable by simple, but quantifiable, hydrological variables, that would include most rivers within a climatic zone. A corresponding number of modeling methods and key predictors could easily be identified and, at the very least, managers would have a starting point for addressing conservation problems.

Model limits

We have intentionally restricted our study to wetlands with low or intermediate disturbance. We have unintentionally constrained our study to the hydrological conditions represented by 18 yr of water level records of the Ottawa River. We could therefore infer that there are other hydrological conditions, not represented by the data from the Ottawa River, where variables other than ld and tsec would be paramount. For example, at extreme values, the mean depth of flooding may become the overriding predictor of the limit of wooded wetland. There are most certainly flood events, not described by our data, that would limit the distribution of wooded wetland. Our model is designed to address a specific problem—the incursion of woody plants in herbaceous wetlands—within the range of variables that is likely to be encountered under current management practices.

One of the weaknesses of our analysis is the problem of site differences. However, the best predictors were consistently tsec in combination with either ld or gs. The two sites that differed significantly, Lucerne Boulevard and Fitzroy Provincial Park, included the extremes of exposed and protected shoreline. This suggests that the model is most accurately applied to intermediately disturbed wetlands. However, when the probabilities of 0.70 and 0.30 were used to delimit wooded wetland, only 18 of the 222 points were incorrectly identified. In short, the general trends are consistent and the accuracy of the model is >70% at its worst site.

Conclusion

Our approach has been, in effect, a study of trait–environment relationships as outlined by Keddy (1992) and illustrated by researchers such as Noble and Slatyer (1980) and Box (1981). The trait used to identify vegetation types is very simple: woody or not woody. The use of vegetation types or functional groups in monitoring changes in wetland vegetation is a well-established practice (Jaworski et al. 1979, Larson et al. 1980, Golet and Parkhurst 1981; M. Jean, M. D'Aoust, L. Gratton, and A. Bouchard, 1992, Institut de Recherche en Biologie Végétal, *unpublished report*). Quantifying the predictors of functional groups (Poiana and Johnson 1993, Auble et al. 1994, Ellison and Bedford 1995) is the obvious next step and is an emerging theme in conservation ecology.

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